Contrasting influences of inundation and land use on the rate of floodplain restoration

Running Head: Inundation and land use affect wetland restoration

Authors: S.K. Dawson, R.T. Kingsford, P. Berney, J.A. Catford, D. Keith, F. Hemmings, J. Stoklosa

Author addresses:

Samantha K. Dawson (corresponding author): samantha.k.dawson@gmail.com Rm 508, Centre for Ecosystem Sciences, School of Biology, Earth and Environmental Sciences, University of New South Wales, Kensington, NSW 2052, Australia

Richard T. Kingsford: Centre for Ecosystem Sciences, School of Biology, Earth and Environmental Sciences, University of New South Wales, Kensington, NSW 2052, Australia

Peter Berney: NSW National Parks and Wildlife Service, Narrabri, NSW 2390, Australia

Jane A. Catford: School of BioSciences, The University of Melbourne, Vic 3010, Australia; Fenner School of Environment and Society, The Australian National University, Canberra, ACT 2601, Australia; Department of Ecology, Evolution and Behavior, University of Minnesota, Saint Paul, MN 55108, USA.

David Keith: Centre for Ecosystem Sciences, School of Biology, Earth and Environmental Sciences, University of New South Wales, Kensington, NSW 2052, Australia

Frank Hemmings: John T. Waterhouse Herbarium, School of Biology, Earth and Environmental Sciences, University of New South Wales, Kensington, NSW 2052, Australia

Jakub Stoklosa: School of Mathematics and Statistics and Evolution & Ecology Research Centre, University of New South Wales, Kensington, NSW 2052, Australia

Author Contributions: SKD, RK, PB, JAC and DK conceived and designed the research, SKD conducted surveys, FH identified species, SKD and JS conducted analysis, SKD, RK, PB, JAC, DK, JS and FH wrote and edited the manuscript.

Abstract: We examined the assisted natural restoration of an Australian floodplain wetland where flows were reinstated and the river was reconnected to the floodplain, following the cessation of agricultural cultivation. We surveyed extant vegetation three times, over an inundation event across a range of sites with different land use histories. Two key opposing factors influenced the success of restoring native floodplain vegetation: inundation and land use. Restoration rate and success increased with increasing inundation frequency but decreased with antecedent land use intensity. Prolonged land use history (>12 years continuous cultivation) restricted restoration success, increasing the persistence of exotics and dryland species, and indicative of an altered stable state considerably different from the restored state. Fields with a short land use history (1-3 years clearing and cultivation) resembled undisturbed floodplain communities, consistent with a “field of dreams” hypothesis. Inundation increased abundance and richness of target wetland species most significantly when there was a high frequency inundation. Our work demonstrated that while river-floodplain reconnections can restore wetland successfully, legacy effects of past land use may limit the pace and outcomes.

Keywords: Environmental flows, vegetation management, ephemeral dryland wetland, alternative states, water regime, flooding

Implications:

- The possibility of development of alternative stable states should be considered when planning wetland restoration, especially when past land use involved high intensity disturbance, e.g. cultivation
- Frequent inundation is essential to ephemeral wetland restoration, with high frequencies increasing restoration rates

Introduction

Governments and community organizations are increasingly trying to restore the historic continuity and structure, species composition and functions of ecosystems by reinstating ecological processes (Clewell & Aronson 2013). For wetlands, restoration often primarily involves manipulation of inundation regimes (assisted natural restoration; Arthington & Pusey 2003; Brudvig 2011) to reinstate as closely as possible historical abiotic conditions, which is consistent with the “Field of Dreams” hypothesis (Palmer et al. 1997). Indigenous vegetation is assumed to sequentially recolonize degraded sites, given removal of the cause of degradation and reestablishment of ecological processes (Palmer et al. 1997; Suding, Gross, & Houseman 2004). Unfortunately, such a simplistic focus can ignore other ecological influences which change restoration outcomes and lead to alternative stable states (Palmer et al. 1997; Suding et al. 2004; Young et al. 2005; Williams et al. 2008; Toth 2010). Exotic species may displace native species (Whalley et al. 2011; Toth & van der Valk 2012) and land use (e.g. agriculture) may severely degrade ecosystems, irrevocably altering soils and destroying seed-banks, making restoration of indigenous vegetation communities impossible (Middleton 2003; Brudvig & Damschen 2011). Alternative state theory (Suding et al. 2004) provides a contrasting view of ecosystem dynamics to the Field of Dreams, allowing for succession to be arrested or diverted from a linear pathway from degraded to desired indigenous states. We tested the applicability of these concepts to the restoration of a wetland ecosystem.

Wetlands are among the most degraded ecosystems worldwide and under continuing pressure (Millennium Ecosystem Assessment 2005). In semi-arid and arid regions of the world, floodplain wetlands have declined in size (>50% worldwide since 1900) and their capacity to deliver ecosystem services, particularly in response to water resource developments upstream (Lemly et al. 2000), increasing the relative importance of the remaining remnants as sites for biodiversity conservation (Nilsson et al. 2005). Management responses to wetland loss include large restoration projects using environmental flows (Kingsford 2011; Pittock & Finlayson 2011). The Australian Government aims to return 2,750GL per year to the environment to restore rivers and wetlands in the Murray-Darling Basin (Murray-Darling Basin Authority 2012). Environmental flows are thus a primary mechanism for restoration and maintenance of highly regulated freshwater ecosystems in Australia (Arthington & Pusey 2003). For example, returning peak flood events in regulated systems can maintain function and composition of vegetation in floodplain wetlands (e.g. River Murray, Catford et al. 2011).

Restoring wetland vegetation using environmental and managed flows reflects a "Field of Dreams" approach to ecological restoration. Yet efficacy of this approach remains poorly understood for many ecosystems, particularly given uncertainty of confounding causes of degradation (Suding et al. 2004; Brudvig & Damschen 2011). Land use history may reduce restoration success for vegetation communities yet it is rarely investigated (Brudvig 2011). We investigated whether a 'Field of Dreams' model adequately explained the response of wetland vegetation to environmental flows or whether land use history compromised restoration success, suggesting possible alternative states. We examined the effects of inundation and land use history on restoration success of historical native vegetation communities in a Ramsar-listed wetland in north-western NSW, Australia. We predicted that restoration rates and success would increase with more frequent flooding and decrease with more time in cultivation.

Methods

Study Region

The Macquarie Marshes is a semi-arid wetland in the Murray-Darling Basin (Fig. 1), one of the more agriculturally developed river basins in Australia (Kingsford 2000; Leblanc et al. 2012). The Marshes are formed from the anabranching channels of the Macquarie River, before it joins with the Barwon River (Yonge & Hesse 2009). They cover about 200 000 hectares, and experience semi-regular spring inundation (Paijmans 1981; Kingsford & Auld 2005; Thomas et al. 2015). The flood-dependent vegetation is adapted to variable flows, surviving dry periods, growing and recruiting with inundation (Brock & Casanova 1997). Historically, annual river flow was highly variable (ranging from 2% to 940% of the mean), but river regulation has reduced the median annual flow to 44.83% of the pre-regulation volume and variation only reaches an upper limit of 300% (Kingsford & Thomas 1995; Ren & Kingsford 2011). The reduced volume and variability of flows have degraded vegetation by replacing native wetland species with dryland and exotic species, and contributed to declines in waterbird and fish populations (Kingsford & Thomas 1995; Steinfeld et al. 2013; Bino et al. 2014; Bino et al. 2015; Catelotti et al. 2015).

There is a mixture of land uses in the Marshes: about 10% is protected within a Nature Reserve (Fig. 1); most remains private land grazed by livestock; and some is dryland and irrigated cropping enterprises. The Pillicawarrina property was one of the largest cropping enterprises, growing wheat and irrigated cotton from the 1980s. Cropping replaced largely intact flood-dependent vegetation communities (Paijmans 1981), including river-red gum forests (*Eucalyptus camaldulensis*), lignum communities (*Duma florulenta*), river cooba

(*Acacia stenophylla)* and a mixed marsh understory (*Eleocharis plana, Ranunculus undosus, Stellaria angustifolia*, etc; pers. Comm., Peter Hall, local grazier at the time, March 2013). Agricultural development occurred in stages over 21 years (1985-2006), across six fields, cleared of native vegetation and sometimes laser-leveled for cultivation (Fig. 1, Table 1). Levee banks were constructed around some fields, with the largest, built in 2002, severing the northern section of Pillicawarrina from the river, preventing inundation of this part of the floodplain (Fig. 1; Lloyd Johnson, Pillicawarrina Property Manager, January 2015, pers. comm.).

In 2008, the New South Wales and Australian Governments bought 2,436 hectares of the enterprise, adjoining Bulgeraga Creek (Fig. 1) and the 8,658ML water license to restore the wetland and provide environmental water for the Macquarie Marshes (Department of Environment Climate Change and Water NSW 2011; Waters 2011). Restoration focused on reinstating inundation regimes to the entire area, beginning in 2009 (Department of Environment Climate Change and Water NSW 2011; Waters 2011; Berney 2012) by breaching levees and improving culverts to reestablish river-floodplain connections (Fig. 1) (Hesse 2009). The goal was to reestablish native wetland vegetation communities, reduce abundances of terrestrial species (native and exotic) and exotic amphibious species (e.g. *Phyla canescens*) (Waters 2011). The area was inundated in 2009/10, 2010/11 & 2011/12, following a decade long drought. We sampled extant vegetation during the 2012/13 inundation event.

Survey methods

We surveyed vegetation at 18 sites: six in the undisturbed Nature Reserve and 12 in the cleared and cultivated fields where land use changed (hereafter referred to as undisturbed or disturbed, Fig. 1, Table 1). Undisturbed sites were not cleared or cultivated and were unaffected by levees. Each of the disturbed sites had different levels of disturbance from past land use, either cleared only or cleared and subsequently cultivated (1-23 times). Sites also had different inundation histories which we measured as either the time since last land use event (given the effect of land use on vegetation) or over a 20 year period since 1992 if the site was undisturbed (1992-2012; Table 1; Thomas et al. 2011, Thomas et al. unpubl. data). Sites disturbed by land use were historically river-red gum forest and lignum shrubland communities, similar to undisturbed sites (Fig. 1.; Paijmans 1981; Kidson et al. 2000).

Two replicate sites were randomly placed in each of six fields, with different clearing-and-cultivation land use histories (Table 1, Fig. 1). We counted and measured the height (shrubs) or diameter at breast height (trees) of all woody species (defined by floras; Royal Botanic Gardens and Domain Trust 2015), rooted inside each 20m x 20m site. We also estimated abundance of herbaceous species within five randomly placed 1m^2 quadrats in each site, using a variation of the point-intercept method, based on a grid of 25 pins (every 20cm) (Hnatiuk et al. 2009). The total number of species' hits that touched each pin provided an estimate of biomass. This index differed from the point-intercept method, which records only one hit per species to calculate an estimate of projected cover (Kent 2012). We surveyed the vegetation three times; every six weeks, across the 2012-2013 inundation and drying cycle, November–March, to assess changes in composition through inundated, drying and dry conditions (Fig. 2).

Data analyses

We examined effects of land use history separately for woody and herbaceous vegetation, accommodating the different survey techniques. We also used functional groupings of herbaceous species, providing a comparative measure for similarly disturbed wetlands with different species (Merritt et al. 2010). Herbaceous species were categorized into 12 functional groups (see Brock & Casanova 1997; Table 2), assigning species on existing data (Casanova & Brock 2000; Porter et al. 2007) or according to life history information (Royal Botanic Gardens and Domain Trust 2015; Table S1). Species were also separated into native and exotic taxa (Royal Botanic Gardens and Domain Trust 2015).

We tested for differences in species' composition among different land uses (i.e. clearing and cultivation history) and inundation treatments, using generalized linear models (GLMs), within the *mvabund* package for multivariate data in R version 3.1.1 (Wang et al. 2012; Warton, et al. 2012; R Development Core Team 2012). The *mvabund* package accounts for varying mean-variance relationships in multivariate response data. We also implemented a resampling approach to account for multiple correlations among response variables (Warton et al. 2012). Before modelling, we removed rare species (single or two observations) to improve computational stability. The response variable was the observed species or functional group abundance (i.e., counts), with two predictor variables fitted to models: the number of years a field was used (i.e. cultivated or cleared; duration of land use) and the number inundations since the last land use disturbance or since 1993 if undisturbed (Table 1). A third predictor, a function of time since last disturbance, accounting for undisturbed sites (*1/number of years since the last land use event*), was excluded from the models because of collinearity between this and years cultivated and years inundated (0.6 and -0.7 respectively). Finally, a negative binomial distribution was fitted to account for heteroscedasticity and overdispersion in the response variable (Bolker 2008). We fitted models for all combinations (additive, interactions and individual), using the two predictor variables, and computed the Bayesian Information Criterion (BIC, Burnham & Andreson 1999) to compare between models. The model with the lowest BIC (the "best model") for each survey period and plant type (herbaceous or woody) was used.

We then calculated univariate statistics, identifying the species and functional groups which contributed most differentiation of communities. To test for significance, an adjusted p-value, from the resampling-based version of Holm's step-down multiple testing procedure, was used to control the family wise error rate across species (Wang et al. 2012). Each survey period was analyzed separately, given that *mvabund* cannot analyze repeated measures, despite its value in dealing with unstable mean-variance relationships.

Results

Floristics

We identified 66 plant species: 91% herbaceous (39 native and 22 exotic), with the remainder woody. The most common herbaceous species included sedges [e.g. flat spike sedge (*Eleocharis plana*) and *Juncus* spp.], grasses [e.g. brown beetle grass (*Diplachne fusca*) and barnyard grass (*Echinochloa* spp.)] and herbs [e.g. slender knotweed (*Persicaria decipiens*), noogara burr (*Xanthium occidentale*) and swamp starwort (*Stellaria angustifolia*)]. The most abundant exotics were noogara burr and wild aster *Aster subulatus* but we also found populations of fleabane (*Conyza bonariensis*), lippia (*Phyla canescens*), and burr medic (*Medicago polymorpha*). Sites with less land use (U1-6, D0-D2) were generally similar to undisturbed sites, with a higher proportion of natives and wetland functional groups, compared to more highly disturbed sites, which had more exotic or terrestrial functional groups (Figs. 3 & 4). As the wetland dried, there was less difference in native composition while the proportion of exotics in undisturbed sites increased (Fig. 4). While overall diversity was similar, more intensively disturbed sites tended to have more terrestrial herbaceous species (Fig. 5). There were 15 exotic species among the 36 terrestrial species, with 10 of the exotic species exhibiting an annual or annual/biennial lifecycle. Terrestrial plant abundance was mostly native (84%, 72% and 61% in the inundated, drying and dried sampling phases respectively) while within exotics, annual or annual/biennial exotics species made up the majority (67%, 62% and 97% respectively).

Most woody species were abundant where they occurred and as were perennial, abundances did not vary over time. The exception was the annual budda pea (*Aeschynomene indica*), which germinated during drying (Fig. 2). River red gum occurred only in undisturbed sites, except for young trees growing along channels of the restoration area. Conversely, *Acacia stenophylla* was the dominant woody species in the restoration sites, occurring in lower numbers in undisturbed sites. Lignum was present in undisturbed and restoration sites, but was in higher abundance and advanced structure in undisturbed sites and therefore of more value to waterbirds.

Compositional response to land use history and inundation

Species' composition was significantly related to years of land use and inundation: both factors were selected in the best and second best models (Table 3). Years of land use was selected in all the best models, across the inundation cycle, for all herbaceous and woody communities. At the beginning of the inundation cycle (inundated, Table 3), number of inundations and years of land use were in the best herbaceous model, whereas, later in the cycle, years of land use alone was the only variable in the best model. Throughout the inundation cycle, results for woody species were similar, not unexpected for mature trees, with even the germination of budda pea not affecting model selection. Models which gave the lowest BIC and contained only the years of land predictor variable were usually within five BIC values of a model containing both: the number of inundations and years of land use predictor variables, suggesting that-both models gave a similar fit to the data. Within herbaceous species' models, the three top performing functional groups accounted for most of the variation observed among sites (see Table 3). Compositional changes largely occurred across land use disturbance and inundation gradients within these functional groups.

Over the full inundation cycle, abundances of the top three native herbaceous amphibious functional groups were negatively related to the years of land use history. In contrast, there was a positive relationship between abundance of exotic dry terrestrial species (3rd strongest functional group) and land use disturbance in the dry phase (Table 3). Alternatively, inundation frequency was positively related to abundance of native and exotic floating-leaved species during the inundation period and negatively related to abundance of native terrestrial damp species (Table 3).

The model coefficients (Fig. 6) showed that functional groups responded differently to disturbance and inundation. Amphibious functional groups were positively related to the inundation frequency, in the herbaceous community, during the inundation period (Fig. 6 a). In contrast, the terrestrial dry functional groups were associated more positively with more intensive land use disturbance. Further, abundances of terrestrial exotics were positively related to the years of land use in the drying phase (Fig. 6b) but abundances of native amphibious functional groups were negatively related to increasing years of land use, albeit not always significant. During the dry phase, only native amphibious functional groups were significantly negatively related to increasing land use. Over the drying period, fewer functional groups were significantly related to the environmental variables than during the inundated period. All woody species had similar coefficient plots (Fig. 6d) but none were significant. River red gum had a large negative coefficient, but confidence intervals were also large. Both budda pea and river cooba records were weakly positively related to the number of years of land use history. Overall, woody species were not strongly related to land use history, although river red gums were not usually found with increasing land use history.

Discussion

We examined the success of a wetland restoration project, requiring significant investment (capital and operating) which relied on returning some of the original inundation regime. The goal was establishment of the original vegetation composition and structure over time. Encouragingly, environmental flows established the functional diversity of targeted native plant species where prior cultivation had not been prolonged. There was more likely to be a positive effect on wetland native species if there were frequent inundation events after cessation of cultivation. Under these conditions, the response to restored flooding was consistent with the “field of dreams” hypothesis, exhibiting a targeted trajectory where history of land use was of short and not a strong driver. Conversely, sites affected by a long history of land use maintained a low functional diversity of wetland native plants during and after the reintroduction of flood waters. This suggests that ‘field of dreams’ restoration responses were either greatly decelerated or arrested by a prolonged period of prior cultivation. The latter is consistent with transitions to alternative stable states, which apparently maintain a stable composition of exotic and/or dryland vegetation despite reinstatement of flooding. Thus, the duration of historical cultivation appears to mediate the restoration trajectories of our wetland plant communities in response restoration of environmental flows, and the likelihood of a field of dreams response is positively related to the inundation frequency of environmental flows. Further, the expression of these responses varied across the inundation cycle. In summary, maximum restoration success may be expected from environmental flows when inundation is frequent and sites have a relatively short duration of land use history.

Our evidence of restoration success, conditional on land use history and subsequent flood frequency contrasts with poor response to restoration efforts in American wetlands (Galatowitsch & van der Valk 1996) and terrestrial woodlands in Australia (Munro et al. 2009; Nichols et al. 2010), where there was little evidence of a 'Field of Dreams' effect. In both cases, restoration was attempted after long histories of intensive land use.

Land use history effects

Although several studies demonstrate strong influences of historical land use on restoration of species' composition (Flinn & Velland 2005; Brudvig & Damschen 2011), few have explored how the duration or intensity of land use disturbance affects restoration. Instead, they rely on static comparisons between past cultivation use with non-cultivated sites (Brudvig 2011). In our study, the duration of intensive land use disturbance (years of clearing and cultivation) was the most important predictor of species' composition in restored fields. It was the dominant predictor alone or with inundation frequency in all our models for woody and herbaceous species, over the full inundation cycle (Table 3). Land use disturbance was negatively related to native herbaceous plant groups, particularly amphibious wetland functional groups. Fields that had experienced prolonged cultivation had a greater proportion of exotic annual terrestrial species than less disturbed sites (Fig. 6). A prolonged legacy of land use disturbance at least reduces the rate of wetland restoration and may inhibit it indefinitely, limiting progress on management goals to restore amphibious native wetland species. The effects were apparent but not as strong for woody species.

Our restored sites, with low land use disturbance, had similar proportions of species (functional grouping and native/exotics) to the reference sites (Figs. 3 & 4), reflecting relatively rapid (5years) progress towards restoration targets. Restoration rates appear to be slower in some other types of large (>100ha) riverine wetlands where at least 20-100 years may be required for significant restoration progress (Galatowitsch & van der Valk 1996; Moreno-Mateos et al. 2012). The status of in situ native soil seed banks and the frequency of inundation probably increased the rate of restoration in our study. Assays of soil seed banks at sites with different disturbance histories could help resolve their role in restoration and compare with seed bank studies conducted just prior to restoration (Waters et al. 2010a). Conversely for sites experiencing prolonged land use, we may only have captured the initial restoration phases, requiring ongoing monitoring to test long-term effectiveness. Alternatively, restoration barriers may be at play, requiring investigation of supplementary management actions (introduction of seed, soil treatments, weed control, etc.) to initiate more favorable responses to environmental flows under those conditions.

Inundation effects

Frequency of inundation was positively related to most native wetland functional groups (Fig. 6) during the inundation, when flows were at their highest (Fig. 2) and less obvious during the drying phases (Fig. 6, Table 3). Inundation frequency was probably important because past floods may have deposited hydrochorus propagules that were triggered to germinate during actual inundation events, when water availability was high (Nilsson et al. 2010). The combination of high flood frequency and water availability during a flood provided ideal conditions for restoration. When the flood dried (Fig. 2), the proportion of exotics generally increased with drying, suggesting that exotics favored increasing drying, during post-inundation germination conditions (Fig. 4). High inundation frequency was important for increased restoration rates or success, but this may only be detectable during actual inundation.

High inundation frequency promotes restoration success (Middleton 2003), primarily because there is more moisture for germination of wetland species (van der Valk et al. 1992; Capon 2007). On the River Murray, inundation was the strongest driver of transition from vegetation communities dominated by exotic annual terrestrials to dominance by perennial native wetland species, despite grazing land use (Lunt et al. 2012). In contrast, we found that effects of land use history outweighed those of inundation (Fig. 4), probably because cultivation has stronger impacts on standing vegetation and seed banks compared to grazing. Importantly though, Lunt et al. (2012) also found that, without regular inundation, exotic annual terrestrial species re-colonized. While the larger proportion of terrestrial species in our study area were natives, the terrestrial exotics that we recorded followed a similar pattern to that observed by Lunt et al. (2012), with exotic terrestrial annuals re-colonizing with drying. Regular inundation will be important to ensure ongoing success of restoration by increasing the abundance of native wetland species and minimizing colonization of exotic species, even against a background of prolonged land use history in some sites.

Restoration management

There is an increasing global focus on restoration of agricultural landscapes (Middleton 2003), especially through managed environmental flows to wetlands. While success was variable, we showed that environmental water allocations were achieving restoration outcomes that were relatively rapid and most effective in fields not seriously affected by detrimental land use. This provides strong evidence of return on investments from Australian governments to purchase dedicated land (Pillicawarrina) and water allocations to the Macquarie Marshes. Similar returns are likely from investments in other connected wetlands. Further inundation is necessary to continue this success and potentially help manage annual exotic terrestrial plants. These conclusions were reinforced by evidence of interactions between flooding history and land use history.

We showed that successful restoration management needs to understand and manage for the legacies of past land use. These detrimental effects could be offset to some degree by more frequent inundation to increase restoration rates. If there is insufficient water available to achieve inundation frequencies required for restoration of floodplain wetlands, management goals need to adapt to an alternative state (e.g. terrestrial ecosystem, see Suding et al. 2004). Our findings suggest that understanding degradation levels is critical to selecting effective restoration techniques and setting realistic restoration targets (Walker et al. 2014). We recorded no recovery of the most intensely cultivated fields during our study, so we cannot predict their likely long-term outcome without further experimentation to determine responses to other management actions and over longer time scales. Ultimately, restoration success of ecosystems is fundamentally underpinned by an understanding of the drivers of previous changes and the matching management actions to restore the ecosystem.

Acknowledgements: We thank our volunteers who assisted with field work: Sylvia Hay, Jessica Hughes, David Hutchinson, Alison Reid, Ray Dawson, Ali Loewen, Ellery Johnson, Stephanie Creer, Svetlana Kotevska, Joanne Ocock and Celine Steinfeld. Funding for field work was provided by NSW National Parks and Wildlife Service and the Peter Cullen Scholarship to SKD, SKD acknowledges support of the Australian Postgraduate Award. JAC acknowledges support from the Australian Research Council (DE120102221) and the ARC Centre of Excellence for Environmental Decisions.

LITERATURE CITED:

Arthington, AH, Pusey BJ (2003) Flow restoration and protection in Australian rivers. River Research and Applications 19(5-6): 377–95

Berney, P (2012) Pillicawarrina; Summary of findings from vegetation surveys 2009 – 2012. New South Wales Parks and Wildlife, Office of Environment and Heritage, New South Wales, Sydney

Bino, G, Sisson SA, Kingsford RT, Thomas RF, Bowen SD (2015) Developing state and transition models of floodplain vegetation dynamics as a tool for conservation decision-making: a case study of the Macquarie Marshes Ramsar wetland. Journal of Applied Ecology 184: 346-356

Bino, G, Steinfeld CMM, Kingsford RT (2014) Maximizing colonial waterbirds' breeding events using identified ecological thresholds and environmental flow management. Ecological Applications 24(1): 142–57

Bolker, BM (2008) Ecological model and data in R. Princton University Press

Bowen S, Simpson S (2010) Changes in Extent and Condition of the Vegetation Communities of the Macquarie Marshes Floodplain 1991-2008. Final Report to NSW Wetland Recovery Program, Department of Environment, Climate Change and Water New South Wales, Sydney

Brock, MA, Casanova MT (1997) Plant life at the edges of wetlands; ecological responses to wetting and drying patterns. Pages 182-192 In: Klomp N, Lunt I (eds) Frontiers in Ecology; Building the Links. Elsevier Science, Oxford

Brudvig LA (2011) The restoration of biodiversity: where has research been and where does it need to go? American Journal of Botany 98(3): 549–58

Brudvig LA, Damschen EI (2011) Land use history, historical connectivity, and land management interact to determine longleaf pine woodland understory richness and composition. Ecography 34(2): 257–66

Burnham KP, Andreson DR (1999) Model Selection and Inference: a practical information-theoretic approach. 1st edition. Springer, New York

Capon, SJ (2007) Effects of flooding on seedling emergence from the soil seed bank of a large desert floodplain. Wetlands 27(4): 904–14

Casanova MT, Brock MA (2000) How Do Depth, Duration and Frequency of Flooding Influence the Establishment of Wetland Plant Communities? Plant Ecology 147(2): 237–50.

Catelotti K, Kingsford RT, Bino G, Bacon P (2015) Inundation requirements for persistence and recovery of river red gums (*Eucalyptus camaldulensis*) in semi-arid Australia. Biological Conservation 184: 346–56

Catford JA, Downes BJ, Gippel CJ, Vesk PA (2011) Flow regulation reduces native plant cover and facilitates exotic invasion in riparian wetlands. Journal of Applied Ecology 48(2): 432–42

Clewell AF, Aronson J (2013) Ecological Restoration; Principles, Values and Structure of an Emerging Profession. 2nd edition. Island Press, Washington

Department of Environment Climate Change and Water NSW (2011) NSW Rivers Environmental Restoration Program Final Report. Department of Environment Climate Change and Water New South Wales, Sydney

Flinn KM, Velland M (2005) Recovery of forest plant communities in post-agricultural landscapes. Frontiers in Ecology and the Environment 3(5): 243–50

Galatowitsch SM, van der Valk AG (1996) The Vegetation of Restored and Natural Prairie Wetlands. Ecological Applications 6(1): 102–12

Grman E, Bassett T, Brudvig LA (2013) Confronting contingency in restoration: management and site history determine outcomes of assembling prairies, but site characteristics and landscape context have little effect. Journal of Applied Ecology 50: 1234–1243

Hesse, P (2009) Geomorphic Mapping for Pillicawarrina Environmental Water Management Plan. Macquarie University for the Department of Environment Climate Change and Water New South Wales, Sydney

Hnatiuk R J, Thackway R, Walker J (2009) Vegetation. Pages 73-126. In: National Committee on Soil and Terrain (eds) Australian Soil and Land Survey Field Handbook. CSIRO Publishing, Canberra

Kent M (2012) Vegetation Description and Data Analysis: a practical approach. 2nd edition. Wiley-Blackwell, Oxford

Kidson R, Witts T, Martin W, Raisin G (2000) Historical vegetation mapping of the Macquarie Marshes 1949 - 1991. New South Wales Department of Land, Water and Conservation, Sydney

Kingsford RT (2000) Ecological impacts of dams, water diversions and river management on floodplain wetlands in Australia. Austral Ecology 25 (2): 109–27

Kingsford RT (2011) Conservation management of rivers and wetlands under climate change - a synthesis. Marine and Freshwater Research 62: 217–22

Kingsford RT, Auld KM (2005) Waterbird breeding and environmental flow management in the Macquarie Marshes, arid Australia. River Research and Applications 21(2-3): 187–200

Kingsford RT, Curtin AK, Porter J (1999) Water flows on Cooper Creek in arid Australia determine 'boom' and 'bust' periods for waterbirds. Biological Conservation 88(2): 231–48

Kingsford RT, Roshier DA, Porter J (2010) Australian waterbirds – time and space travelers in dynamic desert landscapes. Marine and Freshwater Research 61(8): 875

Kingsford RT, Thomas RF (1995) The Macquarie Marshes in Arid Australia and Their Waterbirds: A 50-Year History of Decline. Environmental Management 19(6): 867–78

Leblanc M, Tweed S, Van Dijk A, Timbal B (2012) A review of historic and future hydrological changes in the Murray-Darling Basin. Global and Planetary Change 80-81: 226–46

Lemly AD, Kingsford RT, Thompson JR (2000) Irrigated Agriculture and Wildlife Conservation: Conflict on a Global Scale. Environmental Management 25(5): 485–512

Lunt ID, Jansen A, Binns DL (2012) Effects of flood timing and livestock grazing on exotic annual plants in riverine floodplains. Journal of Applied Ecology 49(5): 1131–1139

Merritt DM, Scott ML, Poff NL, Auble GT, Lytle DA (2010) Theory, methods and tools for determining environmental flows for riparian vegetation: riparian vegetation-flow response guilds. Freshwater Biology 55(1): 206–25

Middleton BA (1998) Wetland Restoration, Flood Pulsing, and Disturbance Dynamic. John Wiley & Sons Ltd, New York.

Middleton BA (2003) Soil seed banks and the potential restoration of forested wetlands after farming. Journal of Applied Ecology 40(6): 1025–34

Millennium Ecosystem Assessment (2005) Ecosystems and Human Well-being: A Framework for Assessment. World Resources Institute, Washington, DC

Moreno-Mateos D, Power ME, Comín FA, and Yockteng R (2012) Structural and functional loss in restored wetland ecosystems. PLoS Biology 10(1): e1001247

Munro NT, Fischer J, Wood J, Lindenmayer DB (2009) Revegetation in agricultural areas: the development of structural complexity and floristic diversity. Ecological Applications 19(5): 1197–1210

Murray-Darling Basin Authority (2012) Basin Plan 2012. Signed by the Minister for Sustainability, Environment, Water, Population & Communities, Murray-Darling Basin Authority, Canberra, Australia

Nichols PWB, Morris EC, Keith DA (2010) Testing a facilitation model for ecosystem restoration: Does tree planting restore ground layer species in a grassy woodland? Austral Ecology, 35(8): 888–897

Nilsson C, Brown RL, Jansson R, Merritt DM (2010) The role of hydrochory in structuring riparian and wetland vegetation. Biological Reviews 85(4): 837–58

Nilsson C, Reidy CA, Dynesius M, Revenga C (2005) Fragmentation and flow regulation of the world's large river systems. Science 308(5720): 405–8.

Paijmans, K (1981) The Macquarie Marshes of inland northern New South Wales. CSIRO, Canberra

Palmer MA, Ambrose RF, and Poff NL (1997) Ecological Theory and Community Restoration Ecology. Restoration Ecology 5(4): 291–300

Pittock J, Finlayson M (2011) Australia's Murray-Darling Basin: freshwater ecosystem conservation options in an era of climate change. Marine and Freshwater Research 62: 232–43

Porter JL, Kingsford RT, Brock MA (2007) Seed Banks in Arid Wetlands with Contrasting Flooding, Salinity and Turbidity Regimes. Plant Ecology 188: 215–34

R Development Core Team (2012) R: A language and environment for statistical computing. R Foundation for Statistical Computing

Ren S, Kingsford RT, Thomas RF (2010) Modelling flow to and inundation of the Macquarie Marshes in arid Australia. Environmetrics, 21: 549–561

Royal Botanic Gardens And Domain Trust (2015) PlantNET - Flora of New South Wales, The Plant Information System Network of the Royal Botanic Gardens and Domain Trust http://plantnet.rbgsyd.nsw.gov.au/search/simple.htm (accessed 15 May 2015)

Steinfeld CMM, Kingsford RT, Laffan SW (2013) Semi-automated GIS techniques for detecting floodplain earthworks. Hydrological Processes 27(4): 579–91

Steinfeld CMM, Kingsford RT (2013) Disconnecting the floodplain: earthworks and their ecological effect on a dryland floodplain in the Murray-Darling Basin, Australia. River Research and Applications 29: 206-218

Suding KN, Gross KL, Houseman GR (2004) Alternative states and positive feedbacks in restoration ecology. Trends in Ecology & Evolution 19(1): 46–53

Thomas RF, Bowen S, Simpson S, Cox S, Sims N, Hunter S, and Lu Y (2010) Inundation response of vegetation communities of the Macquarie Marshes in semi-arid Australia. Pages 139-150. In Saintilan N, Overton, I (eds) Ecosystem Response Modelling in the Murray Darling Basin. CSIRO Publishing, Canberra

Thomas, RF, Lu Y, Cox S, and Hunter S (2010) Inundation Mapping and Monitoring of the Macquarie Marshes. Final Report to the NSW Wetland Recovery Program, Department of Environment Climate Change and Water New South Wales, Sydney

Thomas RF, Kingsford RT, Lu Y, Cox SJ, Sims NC, Hunter S (2015) Mapping inundation in the heterogeneous floodplain wetlands of the Macquarie Marshes, using Landsat Thematic Mapper. Journal of Hydrology 524: 194-213

Toth LA (2010) Unrealized Expectations for Restoration of a Floodplain Plant Community. Restoration Ecology 18(6): 810–19

Toth LA, van der Valk AG (2012) Predictability of flood pulse driven assembly rules for restoration of a floodplain plant community. Wetlands Ecology and Management 20(1): 59–75

van der Valk AG, Pederson RL, Davis CB (1992) Restoration and creation of freshwater wetlands using seed banks. Wetlands Ecology and Management 1(4): 191–97

Walker LR, Hölzel N, Marrs R, del Moral R, Prach K (2014) Optimization of intervention levels in ecological restoration. Applied Vegetation Science, 17(2): 187–192

Wang Y, Naumann U, Wright ST, Warton DI (2012) mvabund - an R package for model-based analysis of multivariate abundance data. Methods in Ecology and Evolution 3(3): 471–74

Warton DI, Wright ST, Wang Y (2012) Distance-based multivariate analyses confound location and dispersion effects. Methods in Ecology and Evolution 3(1): 89–101

Waters C, Nairn L, Melville G (2010a) Seed bank Study of "Pillicawarrina" in the Macquarie Marshes. Department of Environment Climate Change and Water New South Wales, Sydney

Waters C, Nairn L, Melville G (2010b) Influence of cropping and grazing on soil seed bank composition and in-situ vegetation on the 'Pillicawarrina' floodplain, Macquarie Marshes. Pages 116-20. In Waters C, Garden D (eds) Proceedings of the 25th Annual Conference of the Grassland Society of NSW. The Grassland Society of NSW, Inc, Orange, New South Wales

Waters, C (2011) Vegetation Restoration Plan for the Pillicawarrina Floodplain. New South Wales Department of Primary Industries, Sydney

Whalley RDB, Price JN, Macdonald MJ, Berney PJ (2011) Drivers of change in the Social-Ecological Systems of the Gwydir Wetlands and Macquarie Marshes in northern New South Wales, Australia. The Rangeland Journal 33: 109–19

Williams L, Reich P, Capon SJ, Raulings E (2008) Soil Seed Banks of Degraded Riparian Zones in Southeastern Australia and Their Potential Contribution to The Restoration of Understorey Vegetation. River Research and Applications 24: 1002–17

Yonge D, Hesse P (2009) Geomorphic environments, drainage breakdown, and channel and floodplain evolution on the lower Macquarie River, central-western New South Wales. Australian Journal of Earth Sciences 56: S35–53

Young TP, Petersen DA, Clary JJ (2005) The ecology of restoration: historical links, emerging issues and unexplored realms. Ecology Letters 8(6): 662–73

TABLES:

Table 1: Land use disturbance and inundation history of 18 sites sampled for vegetation communities in the Macquarie Marshes (see Fig. 1.), including with six undisturbed sites (U1-6) in the Nature Reserve and 12 restoration sites different land use history (D0-5, a-b. . Sites listed in order, from least to most intensely disturbed by land use history. Frequency of inundation at sites was either the number of inundation events since last land use disturbance or the number of inundations between 1993-2012, sourced from flooding maps generated by Ren et al. (2010).

Site	Land use History	Inundation Frequency (1993-2012)*
U1	Historical grazing	15
U2	Historical grazing	8
U3	Historical grazing	7
U4	Historical grazing	4
U5	Historical grazing	3
U6	Historical grazing	5
D0a	Cleared 2000	3*
D0b	Cleared 2000	3*
D1a	Levelled 2002 & Cultivated 2003	2*
D1b	Levelled 2002 & Cultivated 2003	2*
D2a	Levelled 2006 & Cultivated 2006	2*
D2b	Levelled 2006 & Cultivated 2006	2*
D3a	Levelled 2002 & Cultivated 2002, 2004, 2006	2*
D3b	Levelled 2002 & Cultivated 2002, 2004, 2006	2*
D4a	Levelled 2005 & Cultivated 2005 - 2007	2*
D4b	Levelled 2005 & Cultivated 2005 - 2007	2*
D5a	Cleared 1984 & Cultivated 1985 - 2008	2*
D5b	Cleared 1984 & Cultivated 1985 - 2008	2*

**These inundation frequencies were calculated from the time of last land use*

Table 2: Species were categorized into 12 functional groups of vegetation (following Brock and Casanova, 1997). See Table S1 for species' assignments. Names in parentheses are used as shorthand in this study.

Full Functional Group Name	Description
Terrestrial Dry and Native (TerDryNat)	Complete life cycle where there is no surface water
Terrestrial Dry and Exotic (TerDryExot)	
Terrestrial Damp and Native (TerDampNat)	Complete some or all of their lifecycle on saturated soil
Terrestrial Damp and Exotic (TerDampExot)	
Amphibious Fluctuation Tolerators - Emergent Species and Native (AmphTolEmNat) (no exotics species observed)	Germinates in damp to flooded conditions, tolerates variation in inundation, with basal parts submerged and reproduce above water
Amphibious Fluctuation Tolerators - Low Growing Species and Native (AmphTolLowNat)	Germinates in damp to flooded conditions, tolerates variation in inundation, is low growing and can be submerged
Amphibious Fluctuation Tolerators - Low Growing Species and Exotic (AmphTolLowExot)	
Amphibious Fluctuation Responders - Morphologically Plastic Species and Native (AmphResPlastNat)	Germinates when flooded, reproduces above water and is morphologically plastic in response to inundation
Amphibious Fluctuation Responders - Morphologically Plastic Species and Exotic (AmphResPlastExot)	
Amphibious Fluctuation Responders - Species with Floating Leaves and Native (AmphResFloatNat)	Germinates when flooded, reproduces above water, can grow in damp to flooded conditions and has floating leaves when flooded
Amphibious Fluctuation Responders - Species with Floating Leaves and Exotic (AmphResFloatExot)	

Table 3: Models of woody and herbaceous species composition with lowest BIC values (second best models also reported < 5 BIC points of the best model, NA indicates second best model was not within this range) selected for each period in the inundation cycle, identifying the significant factors (land use, inundation (flood), see Table 1), the percentage of deviance explained (see below), and which functional vegetation groups contributed most to explaining the deviance for each model. There were only three or four woody species used so univariate statistics were not calculated. The % dev – top 3 is the deviance explained by the highest performing three functional groups for each predictor variable, these functional groups are

reported in the next column with + and – indicating statistically significant positive and negative relationship with the predictor variable. Where two predictor variables are present (e.g. the inundated herbaceous data) .a indicates the highest performing functional groups for the first predictor variable and .b the second predictor variable.

Data type	**Sample period**	**1. Best Model, 2. 2nd Best Model**	**p-values**	**% dev - top 3**	**Functional Groups**
Herbaceous	Inundated	1.Flood + Land use, . . 2.Land use + Flood	0.00611, 0.0121	68.5%, 81.6%	+AmphResFloatExot.a -TerDampNat.a, +AmphResFloatNat.a, -AmphTolEmNat.b, -AmphResPlastNat.b, -TerDampNat.b
	Drying	1.Land use, 2.Flood + Land use	0.00211	77.2%	-AmphResPlastNat, -AmphTolLowNat, +TerDryExot
	Dry	1.Land use, 2.Flood + Land use	0.0171	97.2 %	-AmphResPlastNat, -AmphTolEmNat, TerDryExot
Woody	Inundated	1.Land use, 2.NA	0.0271		
	Drying	1.Land use, 2.Flood + Land use	0.00411		
	Dry	1.Land use, 2.Flood + Land use	0.0121		

FIGURES:

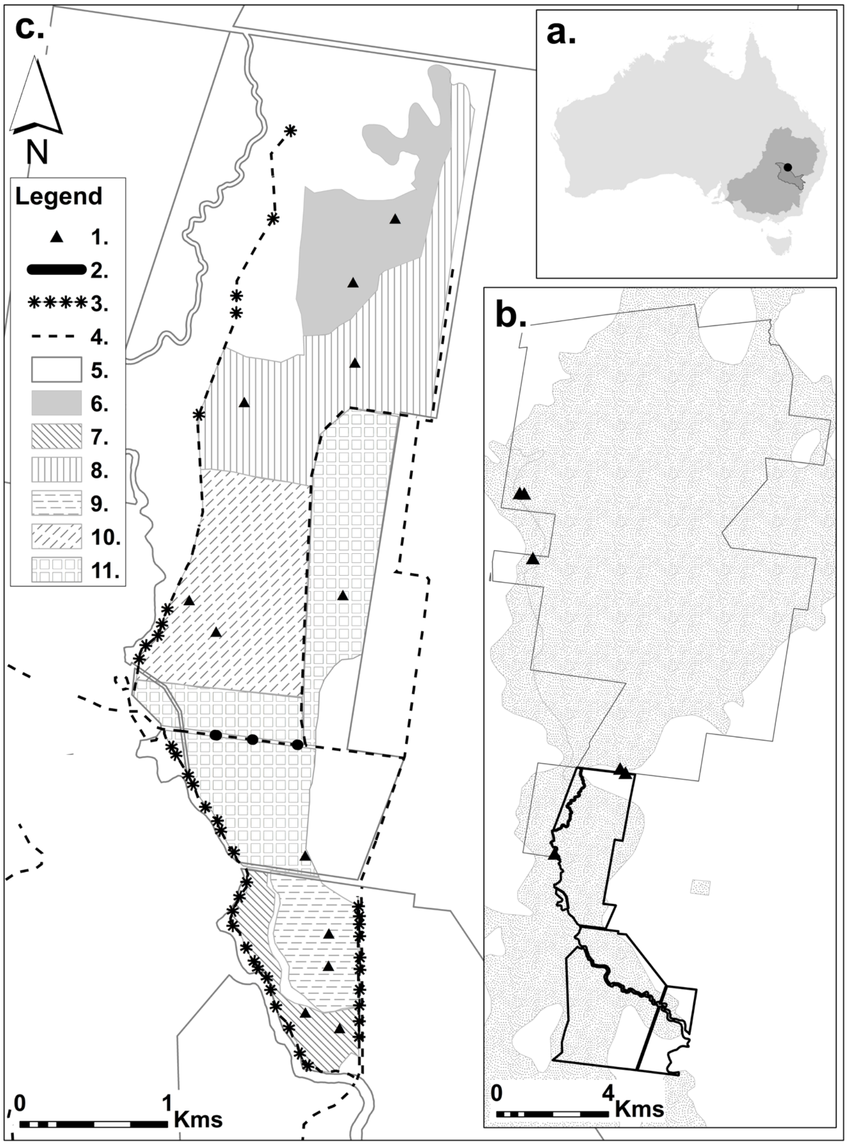

Figure 1: a) Location of the Macquarie Marshes (filled circle), within the Macquarie-Bogan catchment of the Murray-Darling Basin, with b) the Macquarie Mashes Nature Reserve (grey boundary and our restoration site, Pillicawarrina (black boundary) with the regularly inundated area (speckled gray) and c) detailed restoration site with the legend showing survey sites (1) (U1-D5b, see Table 1); culvert improvements (2); levee breaches, mainly along the river (3); levees (4); reserve boundary (5); fields with different land use histories (6-11 see Table 1)

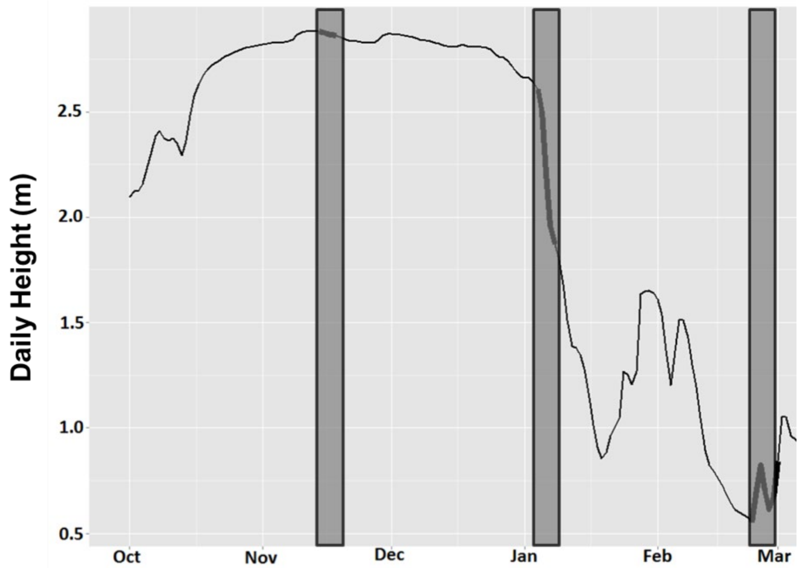

Figure 2: Daily height (m) on the Macquarie River at Pillicawarrina (gauge station number 421147), showing periods of vegetation sampling (grey) during inundated, drying and dry periods (Oct 2012-Mar 2013).

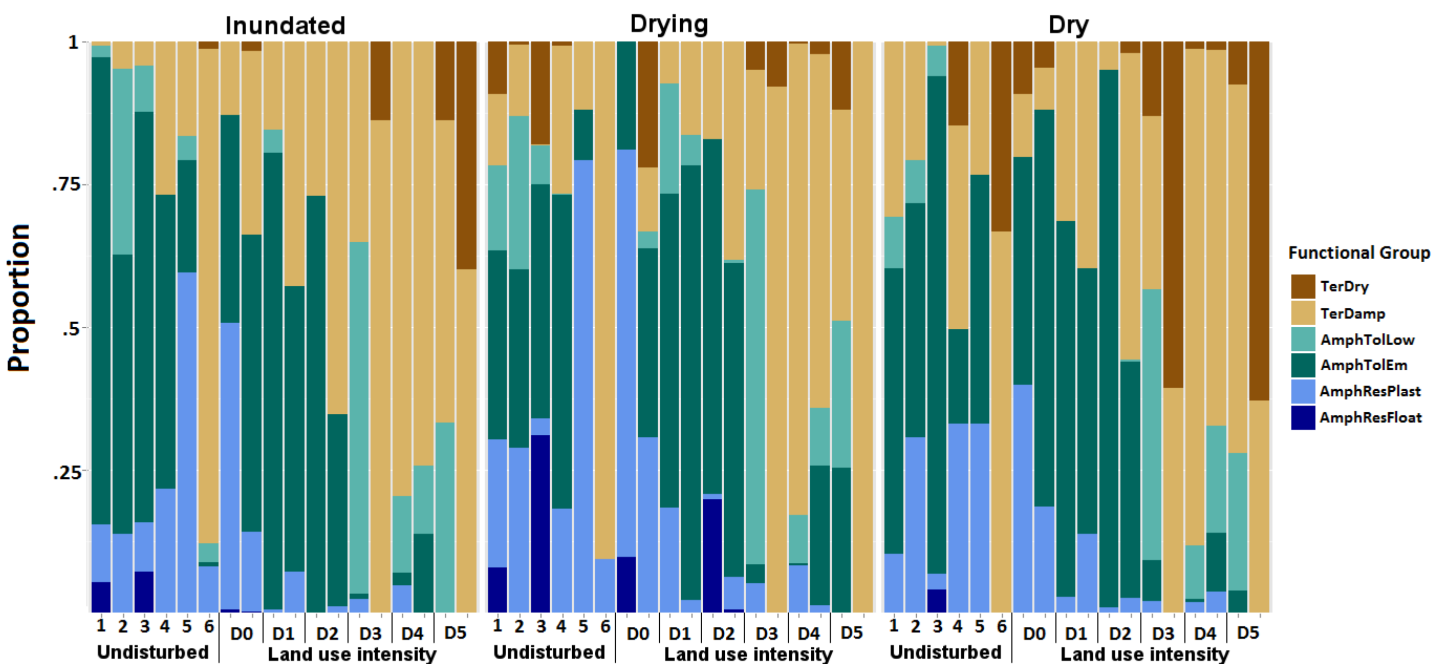

Figure 3: Proportions of herbaceous functional groups (Table 2) at undisturbed survey sites and other sites with increasing land use history (see Table 1) during three sampling periods (inundated, drying, dried) across the inundation cycle.

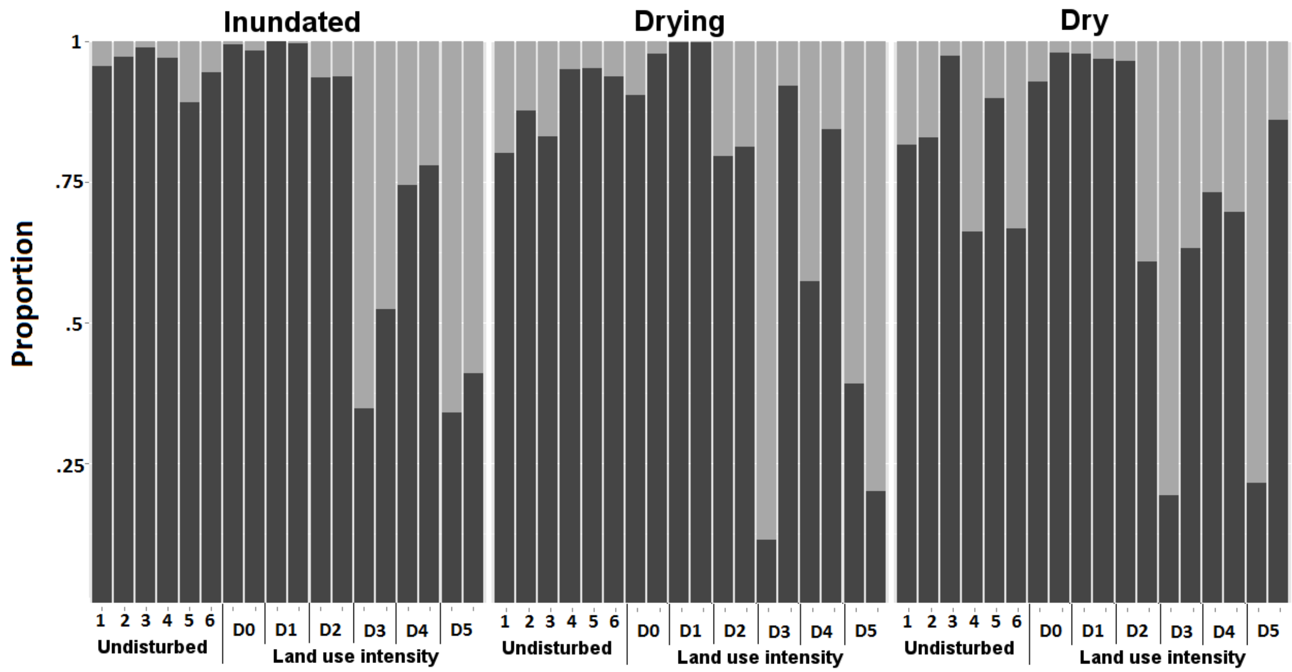

Figure 4: Proportion of the herbaceous native and exotic species at each survey site during three sampling periods across the inundation cycle. Native species are shown in darker gray with exotics in a lighter gray. Survey sites are ordered from least to most disturbed and labelled according to Table 1.

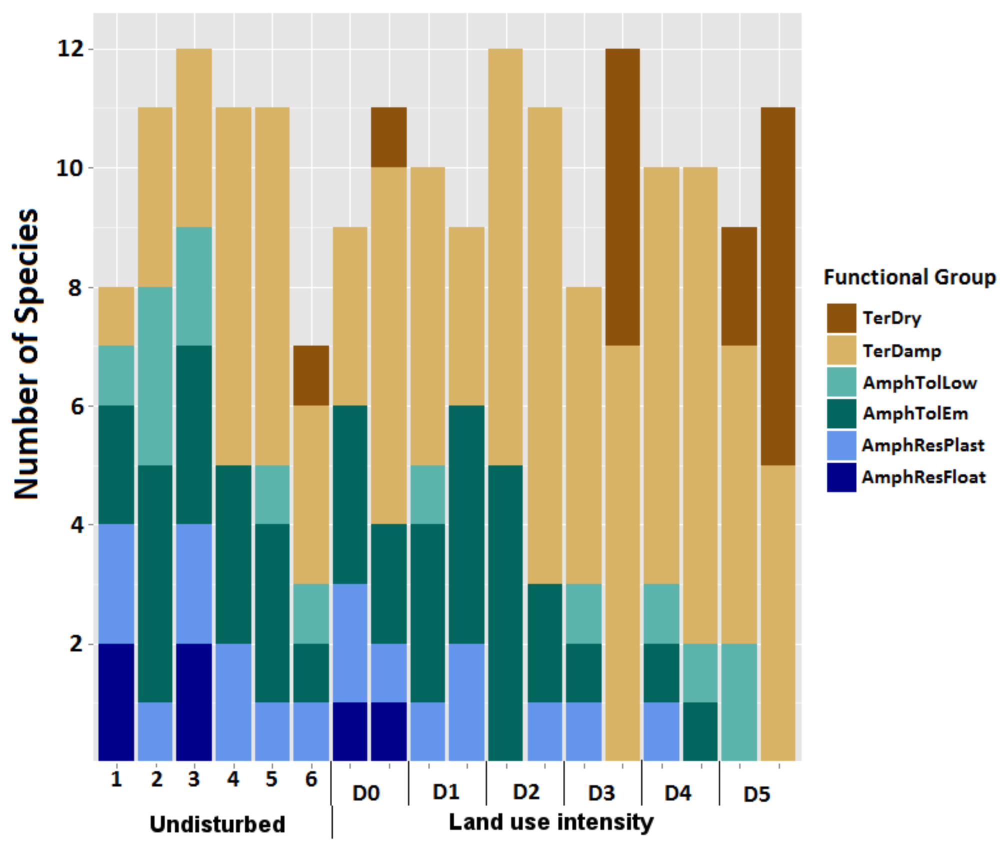

Figure 5: Number of species in the inundated sampling period, shaded by functional groups and bars representing survey site. Functional groups are labelled according to Table 2. Survey sites are ordered from least to most disturbed and labelled according to Table 1.

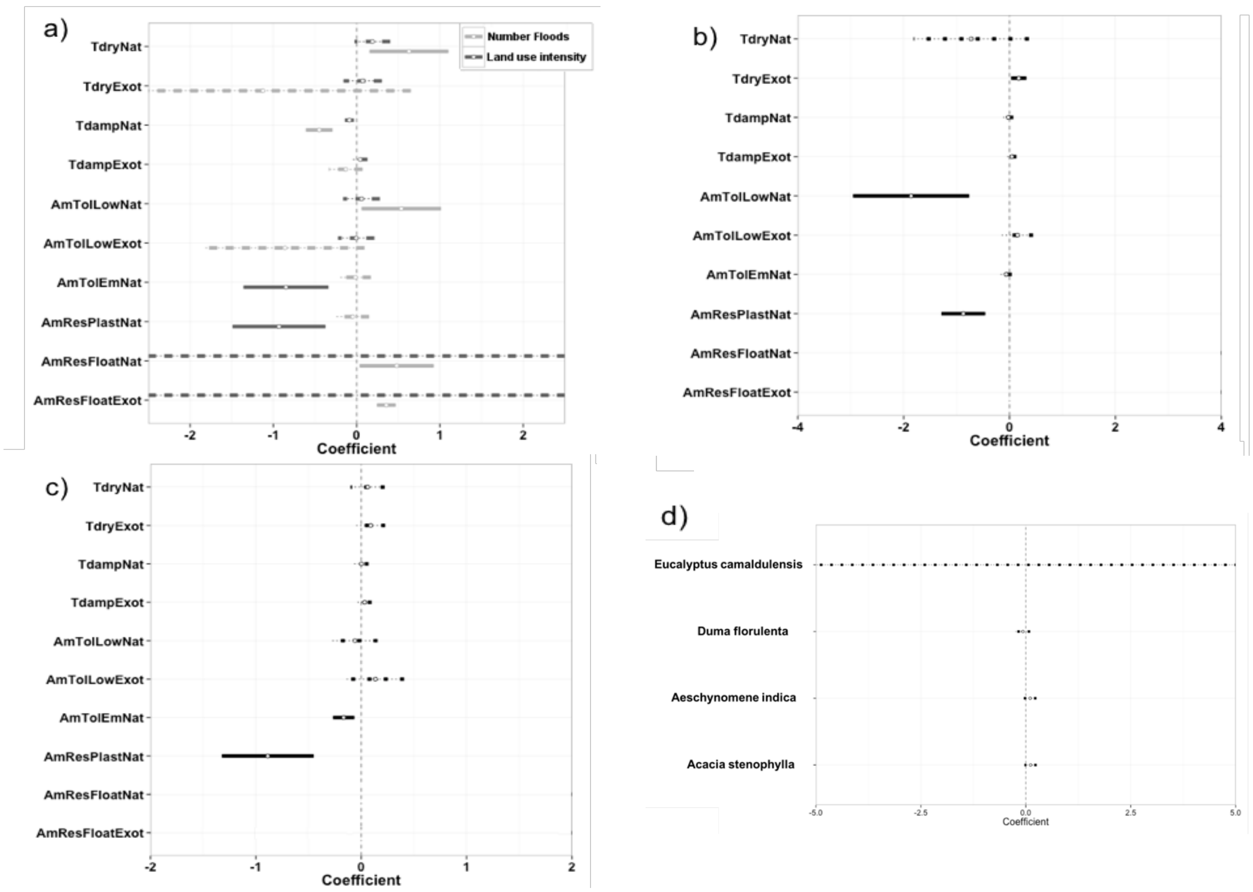

Figure 6: Coefficient plots of slope estimates (±95 % CI) for each functional group of herbaceous species (see Table 2) for the three inundation periods (inundated, drying, dry are a,b,c respectively), showing relationships between the frequency of flooding (grey lines) and land use history (black lines). Coefficient plot of woody species (d) is from the dried period, but all periods were very similar. Significant relationships are indicated where the CI does not cross zero and are represented by solid lines, non-significant relationships are dashed lines.